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Plant species used as wood substrata for nesting by *Megalopta genalis* Meade-Waldo, 1916 and *M. amoena* Spinola, 1853 (Hymenoptera, Halictidae)

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Abstract

Halictine bees are a group that are useful for understanding the evolutionary origins of social behavior and the evolution of nest architecture. Most species nest in the soil, but there have been several evolutionary transitions to nesting in wood. *Megalopta* is a nocturnal genus and represents one of the larger radiations of wood-nesting bees in the Halictinae. These bees have been observed nesting in branches and stems from trees and lianas, but it is not known to which species they belong. There is only a record of a nest in a dead trunk of *Apeiba tibourbou* Aubl. (Malvaceae, Tilioideae). This research aims to identify the wood plant species used as substrata by *Megalopta genalis* and *M. amoena* bees to build their nests. Fieldwork was conducted on Barro Colorado Island. Fifty-nine occupied nests were grouped in 14 morphospecies and anatomically described using transverse, longitudinal and radial sections cut with a microtome following standard histological techniques. Anatomical features of the samples belong to 11 plant species, represented by eight families of angiosperm plants and 11 genera. Considering there are anatomical features that make possible to distinguish trees and lianas like wide vessels, vessel dimorphism, abundance of axial parenchyma and others, we can determine that *Megalopta* bees prefer wood substrates with high proportion of soft tissues from trees or shrubs and possibly mostly liana plant species. The species most used as substrata for nesting were *Uncaria tomentosa* DC. (Rubiaceae), *Hylenaea praecelsa* (Miers) A.C.Sm. (Celastraceae) and *Guettarda* L. (Rubiaceae).

Keywords

Augochlorini, eusocial bees, lianas, sweat bees, wood-dwelling bees

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Introduction

Halictine bees are an interesting group for understanding the evolutionary origins of social behavior (Michener 1990; Danforth and Eickwort 1997; Yanega 1997). Most species nest in the soil, and there are no strong relationships between patterns of soil nest architecture and levels of sociality (e.g., Sakagani and Michener 1962; Eickwort and Sakagami 1979). Some halictid genera have evolved to make burrows and brood cells in dead or decaying plant branches and stems, such as *Augochlora* Smith, 1853, *Xenochlora* Engel, Brooks & Yanega, 1997; three species of *Neocorynura* Schorottky, 1910 and *Megalopta* (Smith 1861; Sakagami 1964; Stockhammer 1966; Sakagami and Moure 1967; Janzen 1968; Eickwort and Eickwort 1973; Schremmer 1979; Engel 2000; Zillikens et al. 2001; Wcislo et al. 2003, 2004; Brosi et al. 2006; Wcislo and González 2006; Tierney et al. 2008a, b; Tierney et al. 2012). The largest radiation of wood-nesting bees involves *Megalopta* Smith, 1853, a genus of approximately 26 large nocturnal bees species that occurs from tropical parts of Mexico to Brazil and northern Argentina (Michener 2000; Moure et al. 2007).

A nest of *Megalopta amoena* Spinola, 1853, was reported by Janzen (1968) inside the stem of a dead branch of *Apeiba tibourbou* Aubl. (Malvaceae, Tilioideae) on the side of a path through a primary forest. The wood anatomy of *Apeiba* Aubl. spp. is characterized by the presence of long multiseriate bands of meta-tracheal parenchyma composed of radially oriented thin-walled cells, which give the wood its typical spongy character and therefore make it soft (den Outer and Schütz 1981). Researchers on Barro Colorado Island (BCI) noted that nests of *Megalopta amoena* could be regularly found in broken vines of a common species, uña de gato *(Uncaria tomentos*a DC.) (W. Wcislo, pers. obs.).

Bees forage for pollen grains from night-blooming trees to avoid competition from diurnal bees, which may compensate for the short bimodal foraging period available for *Megalopta* (Roulston 1997; Wcislo et al. 2004; Kelber et al. 2006; Smith et al. 2012, 2017). This association with some trees as pollen and nectar sources led us to question which woody resources in the forest are used by *Megalopta* bees to build their nests. We asked whether nest substrate selection relates to their food sources or to preferences for specific characteristics of wood selected by *M. genalis* and *M. amoena* for nest building. Since these bees bore into wood with robust mandibles, we assume they need relatively soft wood that can be easily chewed but strong enough to provide them protection (Wcislo and González 2006).

Lianas and vines rely on host trees for structural support (Angyalossy et al. 2015), and their ecology and habitat are reflected in the anatomical features of their wood, making it possible to distinguish them from shrubs and trees. Among these features are the notable wide vessels, vessel dimorphism, long vessel element length, predominantly simple perforation plates, tracheids and vasicentric tracheids, abundance of axial parenchyma, wide rays, long fibers, and cambial variants (Carlquist 1981, 1985, 2001; Fisher and Ewers 1989, 1995; Ewers et al. 1990; Gasson and Dobbins 1991; Putz and Mooney 1991; Rowe and Speck 2005; Angyalossy et al. 2012, 2015; Chery et al. 2020).

The nesting substrata (soil *versus* wood) may influence the propensity to engage in social interactions, especially if suitable wood is a limiting resource (Wcislo 1997;

Danforth and Eickwort 1997). To assess the relative abundance of dead branches, vines, and lianas in a tropical forest, we need to know which tree species have suitable wood for the bees' nesting. We used nests that previously contained *Megalopta* bees and used thin sections of wood to score morpho-anatomical features to identify the plant species that were used as nest substrata.

Materials and methods

Fieldwork was conducted on BCI, which is located in Lake Gatun within the Panama Canal, between the Pacific Ocean and the Caribbean Ocean (9°09'N, 79°51'W). Its vegetation is a semi-permanent humid tropical forest (Knight 1975); on only 1,500 ha of a 50-ha forest dynamics plot, 1,468 species of vascular plants were recorded, and 276 of them are lianas (Pérez et al. 2015).

Nest collections

Nests were collected by Erin Krichilsky on BCI from April to June 2018 by walking through the forest during daytime when bees should be inside the nest, from 9:00 to 15:00 GMT-5. Nests occur in the forest understory, where dead and hanging branches were abundant (Fig. 1A) and could be identified by a circular entrance collar (Fig. 1B) (Wcislo et al. 2004). Throughout the field season, approximately 250 nests were collected for other research questions; not all nests were included in this study because they were either too rotten or damaged. The pieces of wood were labeled with a unique code, which indicates the initial name of the collector, number of nests collected, day, and month (Fig. 1C). Immediately after being collected, the woody pieces were open and only occupied wood sticks were used (Fig. 1D). Bees were identified with Gonzalez et al. (2010) key. Adults and the rest of the inhabitants were used for another research.

Wood preparation and measurements

Fifty-nine wooden nests were grouped into 14 morphospecies; only one was examined per morphospecies. Three disks of about 4 cm in length were obtained from each morphospecies with razor blades and a hacksaw. Two disks were used for sectioning and the others to remove radial chips for maceration using the Jeffrey technique (Jeffrey 1917). The disks were softened in boiling water, cut into thin transverse sections (XS), radial longitudinal sections (RLS), and tangential longitudinal sections (TLS) of 18 to 30 μm using a rotational Leica microtome. Sections were stained with a 1% aqueous solution of safranin and aniline blue in alcohol as a contrast stain and mounted in Permount following Tardif and Conciatori (2015). Some samples were too soft to cut, so they were photographed with a Zeiss Evo 40 scanning electron microscope (SEM) on uncoated samples.

Woods were measured and described following the guidelines of the International Association of Wood Anatomists List of Features for Hardwood Identification (IAWA

Figure 1. Nests collection **A** area with abundant dead stems or branches hanging **B** circular entrance collar **C** wood labeled **D** internal view of an occupied nest, arrows pointing to brood cells.

Committee 1989). Twenty-five measurements were considered for the following features: ray height, rays per millimeter (ten counts), fibre length, vessel element length, tangential diameter of vessels, and vessels per square millimeter. In the case of vessel density, vessels in radial multiples were counted ten times as single vessels, as in Wheeler (1986). ImageJ was used to perform the measurements (Rasband, 2011). Woods were compared using the databases of Insidewood (2004 onwards, https://insidewood.lib.ncsu.edu/search, accessed on 3/3/2019) and Wheeler (2011). Sections were microscopically inspected using magnifications of 4-1000X and photographed with a Nikon DS-Ri1 mounted on a Nikon Eclipse E 600 microscope. For the macroscopic observation, wood samples were polished according to Barbosa et al. (2021) and photographed with a Canon EOS Rebel T7 EF-S camera and a Nikon SMZ 445 stereo microscope.

Results

Thirty solitary and eleven social nests of *Megalopta genalis* (41) and fifteen solitary and three social nests of *M. amoena* (18) bees used dead, woody branches and stems from trees, shrubs, and lianas as substrata to build their nests. These *Megalopta* bees used 11 plant species, represented by 8 families and 11 genera. The dead wood-branches and stems correspond with the anatomy of 7 lianas and 4 trees (Table 1, Fig. 2). The nests collected were moderately hard to soft and nearly crumbling. This made it impossible to characterize three morphospecies and a few anatomical features belonging to two liana species because the tissue was deteriorated.

Liana diagnosis

Diffuse porosity. GROWTH RINGS absent. VESSELS exclusively solitary (>90%) found in *Davilla* sp. *H. volubilis* and *U. tomentosa*. The others also have radial multiples of 2–3 or more than 10 multiples like in *Serjania* sp. and few irregular clusters like in *H. praecelsa*. Simple perforation plates were found in most liana species. However,

Table 1. Plant species used by *Megalopta genalis* and *M. amoena* as wood substrata for nesting.

Family	Genus/Species	Habit	Samples
Rubiaceae	*Uncaria tomentosa* DC.	Liana	22
Celastraceae	*Hylenaea praecelsa* (Miers) A.C.Sm.	Liana	12
Rubiaceae	*Guettarda* L.	Tree	5
Rubiaceae	*Faramea* Aubl.	Tree	4
Combretaceae	*Combretum* Loefl.	Liana	3
Malvaceae, Bytneroideae	*Theobroma* L.	Tree	2
Combretaceae	*Terminalia* L.	Tree	2
Celastraceae	*Hippocratea volubilis* L.	Liana	1
Sapindaceae	*Serjania* Mill.	Liana	1
Dilleniaceae	*Davilla* Vand.	Liana	1
Icacinaceae	*Leretia cordata* Vell.	Liana	1
	Undetermined morphospecies 1		1
	Undetermined morphospecies 2		1
	Undetermined morphospecies 3		3

Davilla sp. with scalariform perforation plates with ≤ 10 bars. Vessels of two distinct diameters are present in all species. Mean tangential diameter of vessels varied from <50 μm to > 200 μm (Table 2, Fig. 3). Vessel density varied from 5–20 vessels per mm^2 to 40–100 vessels per mm^2 (Table 2). Mean vessel element length varied from < 350 – 800 μm (Table 2, Fig. 3). Most liana species had alternate INTERVESSEL PITS; opposite pits in *L. cordata*. Intervessel pits scalariform and opposite in *Davilla* sp. Helical thickening in vessel elements of *H. praecelsa* and *U. tomentosa*. Vestured pits found in *U. tomentosa*. Vessel ray-pits with distinct borders; similar to intervessel pits in size and shape, were found in all species. Ray pits with much reduced borders to apparently simple pits in *Davilla* sp. Gum deposits were found, except for *Combretum* sp. and *H. volubilis*. Vascular tracheids were found, except for *Serjania* sp. FIBRES with distinct border pits (fiber-tracheids) common in the radial and tangential walls were most common. *Serjania* sp. presents simple to minutely bordered pits (libriform fibers). Septate fibres were observed in *H. volubilis* and *Combretum* sp., the others are non-septate. Fibres of *H. praecelsa* are non-septate and septate.

Fibres thin to thick-walled were observed in all species. Fibre length varied from < 900–1600 μm (Table 2, Fig. 3). APOTRACHEAL AXIAL PARENCHYMA diffuse in *Davilla* sp., *Combretum* sp. and *U. tomentosa*.; paratracheal axial parenchyma scanty paratracheal in *H. praecelsa*, *U. tomentosa* sp. *H. volubilis* and *Davilla* sp. Paratracheal axial parenchyma vasicentric found in *Combretum* sp., *H. volubilis*, *L. cordata* and *Serjania* sp. Paratracheal axial parenchyma lozenge-aliform, winged-aliform and confluent found in *Combretum* sp. and *H. praecelsa*. Banded parenchyma with more than three cells wide in *L. cordata* and bands up to three cells side in *Serjania* sp. AXIAL PARENCHYMA cells per strand mostly (5–8), (3–4 strands) found in *H. volubilis* and (over 8 cells) in *Combretum* sp., *L. cordata* and *U. tomentosa*. RAYS width mostly 1 to 3 cells, uniseriate rays found in *Combretum* sp., *H. praecelsa* and *U. tomentosa*; larger rays (4 to 10 seriate) found in *H. volubilis* and *Serjania*; rays (>10 seriate) in *Davilla* sp. and *L. cordata*. Multiseriate portions observed in *U. tomentosa*. Rays of *Davilla* sp.

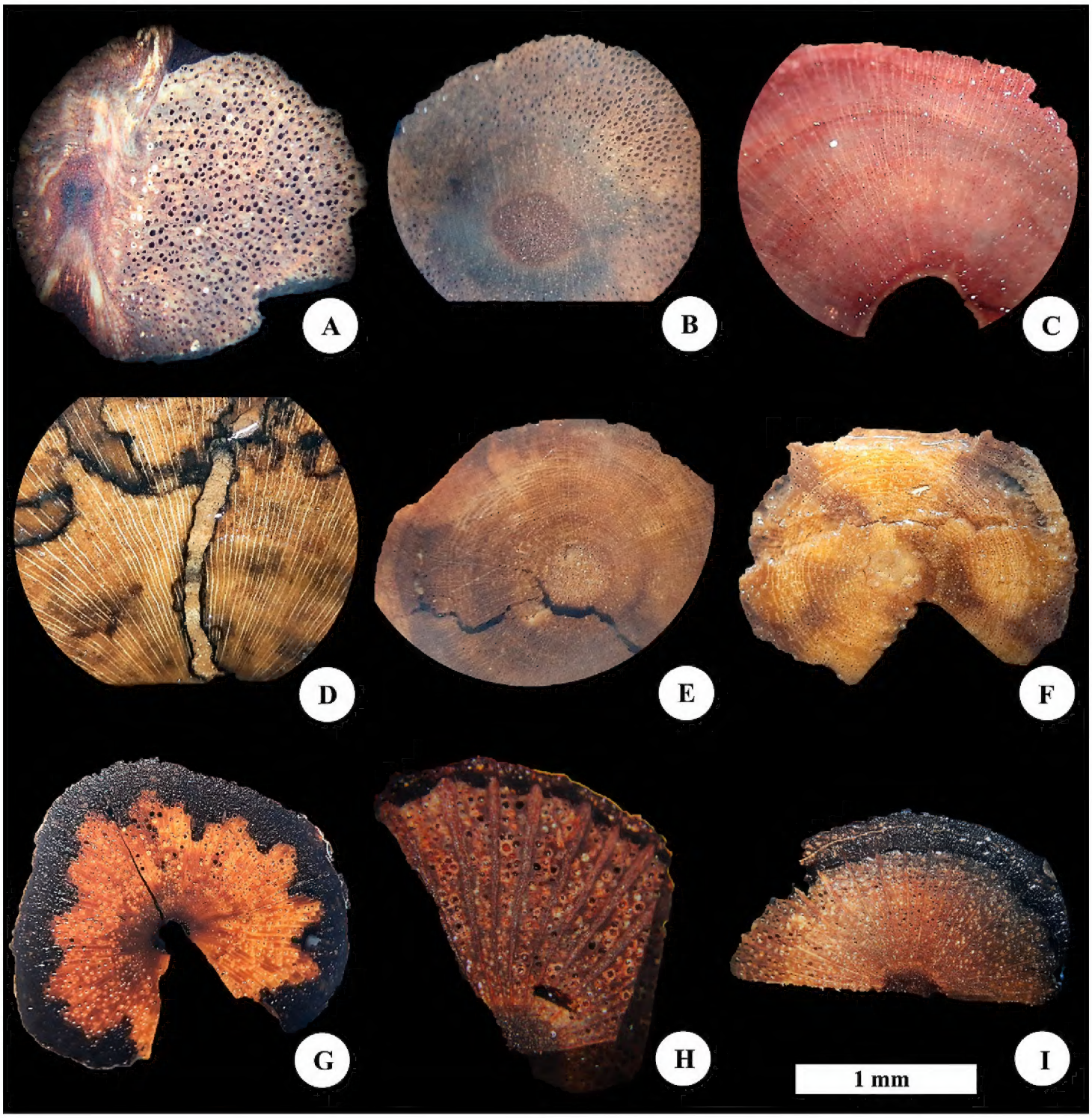

Figure 2. Cross sections of the wood-branches and stems used by *M. genalis* and *M. amoena* **A** stem of *U. tomentosa*, note the anomalous growth to the left (including phloem) **B** stem of *H. praecelsa*, with wide and narrow vessels **C** *Guettarda* sp., note the narrow vessels and the indistinct growth ring **D** branch of *Faramea* sp. note the small vessels and thin rays **E** fissured branch of *Combretum* sp. where the winged aliform and confluent axial parenchyma are observed **F** fissured branch of *Terminalia* sp., with vasicentric, winged and confluent axial parenchyma **G** stem of *H. volubilis*, note the intruding bark and wide vessels **H** *Davilla* sp. stem, note the wide rays and vessels **I** *L. cordata*. stem, note the wide rays and vessels.

H. volubilis, *L. cordata* and *Serjania* sp. with two distinct sizes. Ray height of *Davilla* sp., *H. volubilis*., *L. cordata* higher than 1 mm. Heterogenous rays were common; composed of procumbent cells with mostly 2–4 rows of upright or square marginal cells in *H. praecelsa*, *U. tomentosa* and *Serjania* sp. Rays composed of procumbent cells with 4 rows of upright to square marginal cells in *L. cordata*, *Serjania* sp. and *Davilla* sp. Most of the liana rays are composed of procumbent, square and upright cells mixed throughout the

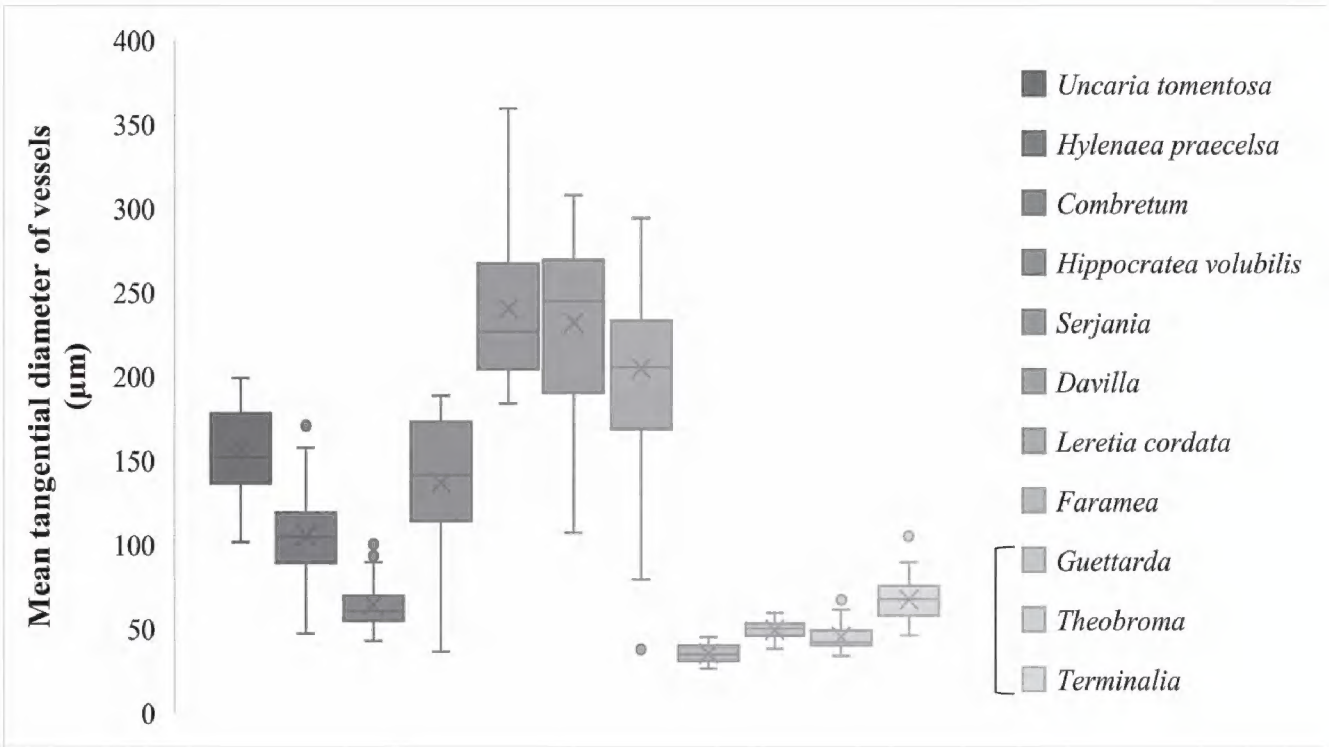

Figure 3. Boxplots showing medians (x) and quartiles. Lianas presents wider vessels, long vessel element length and longer fibres than trees and shrubs (inside de bracket).

Table 2. Features of the stems and branches used by *Megalopta genalis* and *M. amoena* as nesting substrate. Means are given with standard deviations, along with minimum and maximum values. S.V.= solitary vessels; M.T.V.D. = mean tangential vessel diameter. NA = Not applicable.

Morphospecies	Vessel/mm²	S.V. (%)	M.T.V.D. (μ)	Vessel length (μ)	Fiber length (μ)	Ray height (mm)	Rays/mm
Combretum Loefl.	32.7 ± 11.35; 20–59	88.1	64.25 ± 15.30; 42.85–100.31	340.19 ± 118.17; 173.72–596.9	885.58 ± 166.9; 652.86–1284.51	0.54 ± 0.24; 0.22–1.07	12 ± 1.88; 8–14
Davilla Vand.	14.3 ± 2.5; 11–20	100	232.01 ± 48.76; 106.87–307.78	736.49 ± 103.52; 525.22–957.11	1396.46 ± 180.03; 1038.54–1671.63	1.63 ± 1.43; 0.33–3.29	6.4 ± 2.22; 3–10
Faramea Aubl.	61.1 ± 6.06; 51–72	57	35.30 ± 4.97; 26.27–44.96	236.43 ± 69.93; 154.88–386.58	634.11 ± 225.92; 295.37–960.62	1.37 ± 0.54; 0.68–2.31	7.4 ± 2.37; 4–11
Guettarda L.	155.8 ± 31.34; 109–191	48.4	49. 36 ± 5.31; 38.01–59.33	264. 03 ± 94.21; 141.5–492	NA	0.68 ± 0.28; 0.44–1.35	5.7 ± 1.64; 3–8
Hippocratea volubilis L.	25.1 ± 6.90; 14–36	99.4	136.85 ± 42.63; 36.35–188.52	529.54 ± 166.83; 171.59–877.43	1277.55 ± 272.69; 675.41–1630.32	1.08 ± 0.97; 0.22–3.22	5.5 ± 2.92; 2–12
Leretia cordata Vell.	28.9 ± 11.49; 13–50	60.1	204.82 ± 60.04; 37.81–293.99	362.58 ± 74.45; 216.96–462.64	784.57 ± 195.66; 476.39–1251.46	0.82 ± 0.86; 0.25–3.13	7 ± 2.26; 3–12
Hylenaea praecelsa (Miers) A.C. Sm	60.1 ± 7.35; 50–71	86	105.32 ± 28.91; 47.4–170.79	545.35 ± 79.57; 271.64–694.61	886.08 ± 144.34; 587.47–1148.88	0.7 ± 0.30; 0.30–1.26	13.2 ± 2.15; 10–17
Serjania Mill.	20 ± 5.44; 13–29	74.6	240.32 ± 39.63; 183.82–359.08	NA	NA	NA	6.2 ± 1.93; 3–10
Terminalia L.	38.3 ± 11.70; 27–63	48.9	67.26 ± 14.49; 46.06–104.97	437.75 ± 88.04; 240.35–610.36	1210.32 ± 218.97; 726.69–1652.18	1.15 ± 0.61; 0.25–2.48	12.3 ± 1.57; 10–15
Theobroma L.	31.4 ± 7.8; 23-43	47.6	45.18 ± 8.05; 33.87–67.12	305.54 ± 63.23; 156.77-502.58	963.75 ± 200.87; 633–1405. 57	0.86 ± 0.45; 0.34–1.79	5.4 ± 1.07; 4-7
Uncaria tomentosa DC.	42.6 ± 8.13; 31-60	92	156.8 ± 26.85; 101.6–199.1	424.14 ± 4.42; 242.17–539.35	1202.83 ± 220.54; 864.2–1570.75	0.47 ± 0.14; 0.2–0.62	7.5 ± 1.65; 5-10

ray, except in *H. praecelsa*. Ray frequency varied from ≤ 4/mm to ≥ 12/mm rays per mm (Table 2). Rays of two different sizes in *L. cordata*., *H. volubilis*, *Serjania* sp. and *Davilla* sp. Oil or mucilage associated with ray parenchyma in *Davilla* sp. Included phloem observed in *L. cordata* and *U. tomentosa*. Intruding bark observed in *H. volubilis*. Crystals observed, except in *Combretum* sp. and *Davilla* sp. Raphides observed in *Davilla* sp.

Tree diagnosis:

Diffuse porosity. GROWTH RINGS indistinct. *Guettarda* sp. wood has an indistinct formation of growth rings delimited by condensed fibres. VESSELS commonly with 2–4 radial multiples or more like in *Guettarda* sp. Simple perforation plates were found in all species. Mean tangential diameter of vessels varied from ≤ 50 μm to 100–200 μm (Table 2, Fig. 3). Vessel density varied from 5–20 vessels per mm² to ≥ 100 vessels per mm² (Table 2). Mean vessel length varied from ≤ 350 μm to 350–800 μm (Table 2, Fig. 3). All trees and shrubs species present alternate INTERVESSEL PITS. Vestured pits were observed in *Faramea* sp. Vessel ray-pits with distinct borders; similar to intervessel pits in size and shape throughout the ray cell present. Tyloses present in *Terminalia* sp. Gums found in *Faramea* sp. FIBRES thin to thick-walled with simple to minutely bordered pits in all species. Fibres of *Guettarda* sp. and *Faramea* sp. septate;

the other two non-septate. Mean fibre length varied from ≤ 900 μm to 900–1600 μm (Table 2, Fig. 3). APOTRACHEAL AXIAL PARENCHYMA diffuse and diffuse in-aggregates in *Theobroma* sp. Paratracheal axial parenchyma scanty paratracheal in *Guettarda* sp., *Faramea* sp. and *Theobroma* sp. Paratracheal axial parenchyma vasicentric in *Terminalia* sp. and *Theobroma* sp. Also, paratracheal axial parenchyma aliform, lozenge-aliform and confluent in *Terminalia* sp. Banded parenchyma in narrow bands or lines up to three cells wide in *Terminalia* sp. and *Theobroma* sp. AXIAL PARENCHYMA cells per strand mostly (3–4), (5–8 strands) found in *Terminalia* sp. and *Theobroma* sp. RAYS width 1–3 cells and with multiseriate portions as wide as uniseriate portions in *Guettarda* sp. and *Faramea* sp. Larger rays commonly 4 to 10 seriate in *Faramea* sp. and *Theobroma* sp. However, *Theobroma* sp. rays can be >10 seriate, of two distinct sizes and aggregate. Ray height over 1 mm observed in *Guettarda* sp. *Faramea* sp. and *Theobroma* sp. Ray cells heterogeneous, composed of all ray cells upright in *Terminalia* sp. Rays composed of procumbent cells with 1 row of upright square marginal cells in *Guettarda* sp. and *Terminalia* sp. All rays composed of procumbent cells with 2–4 rows of upright marginal cells were the most common. In *Guettarda* sp. and *Faramea* sp. rays were composed of procumbent cells with 1 row of upright marginal cells. Ray frequency varied from ≤ 4 to ≥ 12 rays per mm (Table 2). Sheath cells and raphides present in *Faramea* sp. Crystals present in *Terminalia* sp. and *Theobroma* sp.

Discussion

Wood substrata and bee ecology

Based on the wood substrata analyzed, most bee nests were in lianas. Four plant species, *U. tomentosa*, *H. praecelsa*, *Guettarda* sp. and *Terminalia* sp., were used by both bee species as wood substrates to build their nests; there was no difference between solitary and social bees. *M. amoena* uses stems and branches of smaller diameter than *M. genalis* which was also observed by Wcislo et al. (2004). Curiously, the tree *Faramea* sp. has been used as pollen grain sources by both bee species and, in some years, represents one of the more abundant species in brood cells (Wcislo et al. 2004; Smith et al. 2012).

Anatomical features of wood substrata, nest-site selection, and preference

The wood anatomy of the morphospecies matches anatomical wood features of family, genus and species based on previous descriptions (Dickson 1967; Koek-Noorman 1969; Baretta-Kuipers 1972; Van Vliet 1979; Ter Welle et al. 1983; Menega 1997; Klaassen 1999; Jansen et al. 2001; Jansen et al. 2002; Lindorf 2005; León 2007; Lens et al. 2008; León 2009; Tamaio 2011; Neves et al. 2014; León 2015; Pace et al. 2022). In general, the functional, structural and anatomical features of woody plants are related to plant habit and habitat (Rowe and Speck 2005). Climbing plants have very specific physical characteristics related to their mechanicals properties, the capac-

ity to reach more than 10 m in length or the need to meet the great demand of water that its numerous leaves per unit basal area require, which explains why lianas have wide and long length of vessels and simple perforation plates; it allows an efficient water conduction (Ewers 1985, 1990; Gasson and Dobbins 1991; Putz and Mooney 1991; Angyalossy et al. 2012, 2015; Chery et al. 2020; Meunier et al. 2020).

Wide vessels are susceptible to embolism, which can affect the water flow and cause mortality (Ewers 1990; Urli et al. 2013). A strategy used by lianas in this situation is the narrow or vasicentric tracheids associated with the wide vessels, or the so-called vessel dimorphism that these lianas showed and can be seen in Fig. 3 (Carlquist 1985; Putz and Mooney 1991). Climbing plants also present low density and an intermixed of soft and stiff tissues; the higher abundance of axial parenchyma in lianas in comparison to shrubs and trees is related to their flexibility, storage capacity, and injury repair (Carlquist 1985; Fisher and Ewers 1989; Putz and Mooney 1991; Isnard and Silk 2009). Wide and tall rays are common in lianas; in the families in which ray composition has been studied, these rays are also heterogeneous, and their cells are mixed throughout the rays (Angyalossy et al. 2015). These anatomical features are referred as to the "lianescent vascular syndrome" and together promote effective water conductivity, flexibility and firmness (Carlquist 1985, 2001; Fisher and Ewers 1989,1995; Ewers et al. 1990; Putz and Mooney 1991; Rowe and Speck 2005; Angyalossy et al. 2012, 2015; Chery et al. 2020). However, trees and shrubs or self-supporting plants have narrower vessels, less axial parenchyma, more fibres, higher density, and lower density of vessels per mm^2 like the arborescent species described (Ewers 1985; Baas and Schweingruber 1987; Angyalossy et al. 2015; Chery et al. 2020).

Lianas comprise 35% of the species in tropical forests and 25% of the density of woody stems and constitute habitat and food sources for several animals (Putz 1984; Gentry and Emmons 1987; Schnitzer et al. 2012; van der Heijden et al. 2013; Liu et al. 2021). Climbing plants have narrow stems; they usually have a smaller rate of secondary growth than do trees, and their flexibility is a mechanical advantage for a growth form that may fall from its host (Ewers 1985; Isnard and Silk 2009). The majority of suspended, elevated, or standing dead woods are situated above the forest floor, where they lose as much as 40% of their mass due to water percolating and beginning decomposition before falling to the ground (Swift et al. 1976; Harmon et al. 1986; Gora et al. 2019a). Small branches decompose more slowly when suspended in the understory than when on the forest floor (Harmon et al. 1986; Fasth et al. 2011; Přívětivý et al. 2016). The slower decomposition rates of wood above the forest floor are strongly associated with microclimate and microbial community structure along a vertical forest gradient (Gora et al. 2019b). Based on Gora et al. (2019b) and Marvin and Asner (2016), liana wood debris contributed 2% of total downed wood debris volume, and branchfall ranged over 15–45%, respectively. Rotting branches and stems have a finite existence due to factors such as oceanic sodium deposition, loss of mass from wood during the wet season as decomposition proceeds, or falling to the ground, which would cause faster wood decomposition (Kaspari et al. 2009; Clay et al. 2015; Gora et al. 2019b), possibly causing bees to abandon their nests.

Schnitzer et al. (2012) estimated the stem density of all rooted lianas > 1 cm diameter on a 50-ha Forest Dynamics Plot on Barro Colorado Island, including *H. volubilis* (911), *U. tomentosa* (206), *Combretum* spp. (26 to 882), *Davilla* spp. (659), and *Serjania* spp. (1 to 847) individuals. Some of these species are more likely to be found in the understory. The stems of *U. tomentosa*, however, are not as abundant as those of *H. volubilis* or *Combretum* sp. and even so, they were the most frequently used substrata for nesting. *U. tomentosa* ("cat's claw") is easily recognized by non-botanists by its brown bark, which exfoliates in sheets, and its terminal branches, which are square and have a pair of thorns; these terminal branches are where the bees nest. Although it was the species with the most specimens collected, quantitative data are not sufficient to confirm a preference relative to availability in the forest, and this liana may be overrepresented in collections because researchers know to check this easily-identified species (W. Wcislo, pers. obs.).

Nest architecture and wood-dwelling species

The architecture of *M. genalis* and *M. amoena* nests are similar to those described for other species of this genus (Janzen 1968; Wcislo et al. 2004; Tierney et al. 2008b; Santos et al. 2010; Gonzalez et al. 2014), suggesting that wood nesting is similar throughout the genus, but detailed studies of geographic variation are lacking. The mechanical strength of each of the morphospecies was not evaluated, but it is worth mentioning that some analyzed nests were still firm, which demonstrates these bees have powerful mandibles (Wcislo et al. 2003; Brosi et al. 2006; Santos et al. 2010).

Conclusions

Megalopta genalis and *M. amoena* bees used 11 plant species, represented by 8 families and 11 genera, belonging to 7 lianas and 4 trees. The species more frequently used as substrate for nesting were *Uncaria tomentosa* DC., *Hylenaea praecelsa* (Miers) A.C.Sm., and *Guettarda* sp. Although in some wood morphospecies we only found *M. genalis* bees, in others we found both bee species using the same plant species for nesting.

As previously reported, *M. genalis* and *M. amoena* bees build their nests in the branches and stems of trees and lianas suspended in the understory (e.g., Wcislo et al. 2004). This study shows that anatomical features such as vessel density, vessel element length, mean vessel diameter, vessel dimorphism, presence of wide and high rays, abundance of axial parenchyma, large fibres and vasicentric tracheids are of great help in differentiating wood from lianas or trees. We used these traits to identify the wood in the branches and stems used by *Megalopta genalis* and *M. amoena* bees. *Megalopta* bees prefer wood substrates with high proportion of soft tissues (parenchyma) from shrubs and lianescent plant species that they can bore into with their mandibles, especially lianas. *Uncaria tomentosa* is a distinctive liana with a squared stem that possesses a conspicuous pair of thorns—locally known as "cat's claw" (uña de gato) —and it

was the most selected substrate for nesting in our samples. This result may be biased because researchers are taught lore that bees like these stems, and this liana is one of the few species that a non-specialist can readily identify, so during nest collections, this species may be over-sampled.

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